EFFECTS OF ANIMAL ACTIVITY ON GPS TELEMETRY LOCATION ATTEMPTS

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ABSTRACT: Interpretation of habitat use from GPS collar locations could be biased if the activity of animals wearing GPS collars affects the probability of obtaining a successful location. We tested for this bias with GPS location attempts made by collars deployed on free-ranging moose (*Alces alces*) in northern Minnesota, USA. We classified moose as being either inactive or active during each GPS location attempt based on activity counts recorded by the collar. Only 69% of GPS location attempts were successful while moose were active, compared to 88% when moose were inactive. Moose activity reduced success of location attempts in both summer and winter. We also estimated the precision of GPS locations while collars were deployed on free-ranging moose. When moose were inactive 50% of 3-dimensional locations were within 5 m of the estimated location, and 95% were within 17 m of the estimated location. When moose were inactive, 50% of 2-dimensional locations were within 7 m of the estimated location, and 95% were within 26 m of the estimated location. Despite the bias induced by animal activity, GPS telemetry is the most precise method currently available to obtain locations of free-ranging large mammals such as moose. Sampling biases in GPS units resulting from animal activity should be accounted for when interpreting habitat use by free-ranging animals.

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It is necessary to determine locations of free-ranging animals in order to understand how animals use their habitat, and to understand the consequences of human activities and resource extraction on free-ranging populations. GPS telemetry collars provide temporally and geographically precise locations of free-ranging animals. Benchmark testing of GPS collars established that locations that are not differentially corrected conformed to accuracy specifications of the GPS system (Rempel et al. 1995, Moen et al. 1996b, Edenius 1997). These experiments were all conducted before Selective Availability (SA, the purposeful degradation of GPS signal quality by the U.S. military) was removed. Differential correction, which removed SA's effect, resulted in 95% of locations being less than 10 - 50 m away from the true position (Moen et al. 1997, 1998; Rempel and Rodgers 1997), depending on experimental conditions such as satellite acquisition, vegetation canopy, and the settings used in the differential correction program. In addition, the investigator may use rules such as DOP cutoff values to censor locations that will affect reported precision. As long as SA is not imposed, locations that are not differentially corrected are similar in precision to locations that were differentially corrected with SA in effect (C. Dussault, Département de Biologie, Université Laval, personal communication).

Evaluation of collar performance under different canopy conditions has been limited to collecting a series of GPS locations over short time intervals with a stationary collar at known geographic locations. These short time intervals may also have affected the ability of the GPS unit in the collar to obtain a successful location. The probability of stationary collars obtaining successful locations is reduced under dense or high tree canopies (Rempel et al. 1995, Moen et al. 1996b, Dussault et al. 1999) and is also lower in fall than winter (Dussault et al. 1999). The probability of successful locations under dense tree canopies was also reduced in a GPS collar being worn by a moose under direct observation (Moen et al. 1996b).

Initial observations suggested that moose activity did not affect the probability of obtaining a successful GPS location (Moen et al. 1996b) but most of these observations were carried out under relatively open canopy conditions. A collar carried by a walking human was less likely to obtain positions while underneath a dense forest canopy than a stationary collar (Edenius 1997). Collars worn by moose were less likely to obtain successful locations in some months, and there were differences between day and night in summer (Dussault et al. 1999). Interestingly, GPS collars made by a different manufacturer and tested on white-tailed deer (*Odocoileus virginianus*) obtained more positions when the deer were active (Bowman et al. 2000). Collectively, these results suggest that the probability of obtaining successful GPS locations could be biased by animal activity, the species a collar is placed on, and by collar manufacturer.

The precision of locations could also affect the apparent selection of cover types while collars are deployed on free-ranging animals. During periods when a collared moose under direct observation was bedded, precision conformed to GPS locations that are not differentially corrected before removal of SA (Moen et al. 1996b). The only estimate of accuracy from collars deployed on free-ranging animals is a 95% CEP (Circular Error Probable, or the expected distance within which 95% of locations would be) of approximately 44 m for differentially corrected locations (Moen et al. 1997, 1998).

We used GPS location attempts from 6 collars deployed on moose in Voyageurs National Park in northern Minnesota to determine the effect of animal activity on the success of GPS location attempts and to estimate precision of GPS locations from collars deployed on free-ranging animals. The work reported here is particularly valuable because in most applications of GPS collars it is not possible to determine if free-ranging animals are active or inactive when the GPS locations are being taken. The specific questions we address are: (1) if the activity of an animal alters the probability of success of a location attempt; (2) if there is a relationship between length of activity period and success of a location attempt; (3) if the frequency of GPS location attempts affects the probability of obtaining a successful location; and (4) if the expected precision of GPS locations while collars are on free-ranging moose is worse than the observed precision of stationary collars at benchmark locations. Answers to these questions will help interpret habitat use of free-ranging animals obtained from GPS telemetry locations.

METHODS

Collar and Software

Locations of 6 free-ranging moose fitted with Lotek GPS_1000 differential mode collars (Lotek Engineering Inc., Newmarket, Ontario, Canada) were collected from 1995 to 1998 in Voyageurs National Park in northern Minnesota, USA (48° 30′ N, 92° 55′ W). Collars were deployed in February of 1995, 1996, and 1997. Helicopter netgunning was used in all 3 years to capture and collar moose (Carpenter and Innes 1995). No capture-related mortality of moose occurred. Collars collected GPS locations for 3 - 8 months in 1995, 3 - 11 months in 1996, and 3 - 12 months in 1997 before failing prior to their expected life of 12 months. Intervals between location attempts on moose were either 10 minutes or 4 hours. Collars obtained GPS locations at 4-hour intervals. In addition, each collar was also set to obtain GPS locations at 10-minute intervals for 1 day every 2 weeks (February - April 1995) or every 3 weeks (May 1995 - January 1998). We used the 10-minute intervals for analysis of precision of locations and potential bias caused by animal activity. We used the 4-hour intervals in combination with the 10-minute intervals to analyze relationships between frequency of location attempts and successful locations.

Procedures for downloading data from these collars have been described elsewhere (Rodgers and Anson 1994, Moen et al. 1996b). Differential correction was performed with N3WIN v. 2.20 (Lotek Engineering, Newmarket, Ontario, Canada). Base station data were collected from a Trimble 4000 community base station (Trimble Navigation Limited, Sunnyvale, California, USA) located in Minneapolis, Minnesota from February 1995 to 15 June 1996. This base station was about 375 km from the moose in Voyageurs National Park. These base station files were converted to RINEX format using Dat-Rinx v. 1.0 (William Ehrich, Minneapolis, Minnesota, USA). Base station data from 16 June 1996 to January 1998 were collected with a Novatel 3051 base station (Novatel Communications Limited, Calgary, Alberta, Canada) located at Voyageurs National Park headquarters in International Falls, Minnesota. This base station was about 30 km from the collared moose. These base station files were converted to RINEX format using Convert v. 2.10 (Novatel Communications Limited, Calgary, Alberta, Canada). GPS locations calculated by each base station were similar. The choice of base station was determined by availability of data. We converted latitude-longitude locations (NAD83 datum) to the UTM coordinate system (NAD27 datum) with ArcInfo (v. 7.0, Environmental Systems Research Institute, Redlands, California, USA).

A 3-dimensional position is calculated using 4 or more satellites, while a 2-dimensional position uses 3 satellites. If fewer than 3 satellites are found a GPS location cannot be calculated (Wells 1986, Hurn 1989). User-defined settings that can affect the precision of GPS locations were implemented in N3WIN v. 2.20. These settings include allowing the user to set the Horizontal Dilution of Precision (HDOP) at which a 3-dimensional position is forced to be a 2-dimensional position. HDOP is an indicator of satellite geometry and expected precision of a location. We considered 3-dimensional positions with HDOP ≤ 20 to be successful. The HDOP cutoff of 20 was based on an analysis of the relationship between HDOP and distance from true location in benchmark tests (R. Moen, unpublished data). If a 3-dimensional position had HDOP > 20, or if only 3 satellites were acquired, a 2-dimensional position was calculated. The height estimate used when calculating the 2-dimensional position was an average of the 5 previous heights from 3-dimensional positions with HDOP ≤ 20. If the 2-dimensional position had a HDOP > 20, or if < 3 satellites were acquired, the location attempt was a failure.

Determining Activity of Moose

The GPS_1000 collars use an activity count sensor that is scaled in arbitrary units from 0 to 255 (Moen et al. 1996a, 1997). The activity count is a reliable measure of whether the moose is active or not if activity count intervals are not averaged (Moen et al. 1996a). The activity count is conservative in that errors are likely to be classifying inactive animals as active, rather than active animals as inactive. We classified each 10-minute interval as either active or inactive based on the activity count registered for that 10-minute interval and the adjacent 10-minute intervals. The threshold for classifying an interval as active was set at 20 in 1995 and 1996, and 50 in 1997, based on visual inspection of series of activity counts. The different thresholds for classifying an interval as active may have been due to changes in collar hardware among years. On days when snow depth at the International Falls airport weather station (located < 1 km from the base station) was < 10 cm, we increased the threshold by 10 to 30 in 1995 and 1996, and 60 in 1997. While a 10-cm snow depth will not impede movement of moose, it may alter foraging behavior and the increase in the threshold of 10 units was supported by visual inspection of selected activity count series. We believe that the errors in classifying the moose as active or inactive if this threshold increase were not used would be worse than errors induced by the use of the admittedly arbitrary threshold.

At times the activity count is below the threshold even when moose are active, and at times there are high activity counts within an inactive period (Moen et al. 1996a). Therefore, we devised a set of hierarchical rules to classify each 10-minute interval. The first rule, which applied to 90.6% of 10-minute intervals, was to classify the middle of 3 adjacent activity counts that were above or below the threshold as active and inactive, respectively. The second rule, which applied to 3.5% of 10-minute intervals, was that when a series of low activity count intervals was interrupted by a single high activity count the interval with the high activity count was classified as inactive. Similarly, if a series of high activity count intervals was interrupted by 1 low activity count interval, the interval with the low activity count was classified as active. The third rule of classifying alternating high and low counts as active accounted for 4.4% of location attempts. Intervals at the start and end of a day, when neighboring activity counts could not be used, accounted for 1.6% of location attempts and were classified based on the threshold as defined above. We chose not to use the single neighbor for these locations because over 90% of locations with neighbors were either above or below the active/inactive threshold. Programming code used to implement these rules is available from the senior author.

We determined the effect of moose activity on the probability of obtaining a successful GPS location using the classification procedure described above and a χ^2 test during leaf-on (16 May - 30 September) and leaf-off (1 October - 15 May) periods. Within each active and inactive period we determined whether location attempts that were early in the active and inactive periods were more likely to be successful than location attempts that occurred later. We also compared the probability of obtaining a successful location on days when locations were taken every 10 minutes to days when locations were taken every 4 hours with a χ^2 test. Finally, we used periods of inactivity > 50 minutes to determine the precision of GPS locations while collars were on free-ranging moose.

"True" Locations

It is necessary to estimate the "true" geographic location to determine the precision and bias of GPS locations. Determining the "true" geographic location is relatively easy when the collar is stationary on a benchmark. However, when collars are on free-ranging moose at bedding sites that are not physically located, alternative methods must be used. For days in which we collected GPS locations at 10-minute intervals, we selected all inactive periods longer than 50 minutes.

We used the mean of locations within a single inactive period as the "true" location when there were ≥ 5 3-dimensional differential mode locations with HDOP ≤ 5. The 50% CEP of these "true" locations is likely to be > 2 and < 5 m from their actual geographic location (Trimble Navigation 1992). We experimented with several combinations of different fix qualities in an attempt to determine how precision decreased when GPS locations of poorer quality were used to calculate the "true" location.

RESULTS

Effect of Activity on Location Success

Activity of moose reduced the probability of obtaining a successful GPS location ($\chi^2_1 = 1{,}623$, $P < 0.001$). Overall, 88% of 15,196 location attempts when moose were inactive and 69% of 12,977 location attempts while moose were active, were successful. Collars on individual moose ranged from 78 - 95% successful when moose were inactive, and from 62 - 80% successful when moose were active. Under leaf-off conditions the percentage of successful locations was 90% (SD = 4, range 85 - 95) and 71% (SD = 5, range 64 - 80) for inactive and active periods, respectively. Under leaf-on conditions, the percentage of successful locations was 85% (SD = 3, range 80 - 89) and 66% (SD = 5, range 59 - 74), respectively.

Table 1. Number of satellites acquired when moose were active (*n* = 12,977) and when moose were inactive (*n* = 15,196).

Satellites	Active (%)	Inactive (%)
0	10	2
1	7	2
2	11	5
3	40	29
4	21	36
5	9	21
6	2	6

The cause for the reduced success of location attempts during active periods was a reduction in satellite acquisition (Table 1). When moose were inactive ≤ 2 satellites were found in 9% of location attempts, compared to 28% of location attempts when moose were active. Conversely, ≥ 4 satellites, required for a 3-dimensional location, were acquired in 63% of location attempts when the moose were inactive, compared to only 32% of location attempts when the moose were active. Overall, ≥ 3 satellites were obtained in 91% of the location attempts on inactive moose and in 72% of the location attempts on active moose.

Effect of Activity Period Length

The probability of obtaining a successful location at each 10-minute interval within a bout changed little, ranging from 88 to 91% when moose were inactive and 62 to 71% when moose were active. There was no effect of bout position on success rate for the first 9 10-minute intervals when the moose were inactive ($\chi^2_8 = 13$, $P = 0.12$). When the moose were active, successful locations were more likely after 60, 80, and 90 minutes ($\chi^2_8 = 28$, $P < 0.001$), possibly because we could not precisely identify the end of an active period.

Effect of Location Attempt Frequency

The frequency of successful location attempts declined when locations were collected at 4 hour intervals under leaf-off ($\chi^2_1 = 31$, $P < 0.001$) and leaf-on ($\chi^2_1 = 36$, $P < 0.001$) conditions compared to when locations were taken every 4 hours along with intervening 10-minute locations (Table 2).

Precision of Locations on Moose

When moose were inactive, 50% of 3-

Table 2. Effect of frequency of location attempts on successful location attempts during leaf-on and leaf-off conditions. We compared the probability of obtaining a successful location on days in which locations were taken every 4 hours to the probability of obtaining successful locations taken 4 hours apart (0400, 0800, 1200, 1600, 2000, and 2400) when location attempts were being made at 10 minute intervals.

	Leaf-off		Leaf-on	
	4 hr-day[1]	10-min day[2]	4-hr day	10-min day
Successful	72	81	59	73
Failure	28	19	41	27
n	9,812	734	8,006	460

[1] Location attempts made every 4 hours with 4-hour intervals between location attempts.

[2] Location attempts made every 4 hours on days in which locations were taken at 10-minute intervals.

dimensional locations were within 5 m and 95% were within 17 m of the estimated "true" position (bottom row of Table 3). The precision of 2-dimensional positions was slightly worse, with 50% within 6.5 m and 95% within 25.5 m of the estimated "true" position. The small decrease in CEP error estimates as positions with higher HDOP were eliminated indicates that HDOP values as high as 20 can be allowed with little loss of precision to calculate the "true" position or to calculate CEP error estimates.

However, the relatively small increase in CEP when locations with a HDOP > 10 are included masks a larger loss of precision because there are proportionately fewer locations with HDOP > 10. Positions with HDOP > 10 were less precise than positions with HDOP ≤ 10 (Table 4). Precision of 3-dimensional positions with HDOP between 10 and 20 was similar to precision of 2-dimensional positions with HDOP ≥ 10. The 95% CEP of 2-dimensional positions

Table 3. The 50 and 95% Circular Error Probable (CEP) for 2-dimensional and 3-dimensional locations for inactive periods in which at least 5 successful locations were obtained. The "true" location was the mean x,y of all successful location attempts meeting Horizontal Dilution of Precision (HDOP) criteria in column 1. Mean x,y was based on 5 - 10 successful GPS locations and the CEP values were based on the distance of ≥ 3,677 successful GPS locations from their respective "true" location.

	3-dimensional		2-dimensional	
HDOP criteria used to include positions in calculation of the "true" location	50% CEP (m)	95% CEP (m)	50% CEP (m)	95% CEP (m)
3-dimensional with HDOP ≤ 5.0	4.5	15.0	6.5	24.5
3-dimensional with HDOP ≤ 10.0	4.5	15.5	6.5	24.5
3-dimensional with HDOP ≤ 20.0	4.5	16.0	6.5	26.0
3- and 2-dimensional with HDOP ≤ 20.0	5.0	17.0	6.5	25.5

Table 4. Comparison of the precision between locations with high and low Horizontal Dilution of Precision (HDOP) values. The 50 and 95% Circular Error Probable (CEP) for 2-dimensional and 3-dimensional locations with HDOP ≤ 10 and with HDOP > 10 and ≤ 20 for inactive periods in which at least 5 successful locations were obtained. The "true" location was calculated from the mean *x,y* location. *n* refers to the number of locations used to calculate CEP values.

Type of position	*n*	HDOP	50% CEP (m)	95% CEP (m)
3-dimensional	7302	≤ 10	4.5	15.0
	898	> 10 and ≤ 20	7.0	27.0
2-dimensional	4229	≤ 10	6.0	22.0
	229	> 10 and ≤ 20	17.0	54.0

with HDOP > 10 was more than 50 m.

The altitude from the 3-dimensional differentially corrected GPS locations was similar to the mean altitude. For 3-dimensional positions with HDOP ≤ 10, 50% of altitudes were within 5.5 m of the mean value, and 95% were within 10 m of the mean altitude. For positions with HDOP between 10 and 20, 50% of altitudes were within 21 m of the mean altitude, and 95% were within 43 m of the mean altitude.

DISCUSSION

Ecologists have long searched for a precise and unbiased method to determine locations of free-ranging animals. GPS telemetry is currently the most precise solution available and locations are geographically unbiased in stationary collars not deployed on animals (Moen et al. 1997, Rempel and Rodgers 1997). Our analysis of GPS location attempts from 6 free-ranging moose in northern Minnesota supports Edenius' (1997) suggestion that collar movement reduces the percentage of successful location attempts under a forest canopy. The bias induced by moose behavior, specifically an under-representation of areas where moose are active compared to areas where moose are inactive in both winter and summer, should be considered when interpreting habitat selection by moose from GPS collar locations.

The amount of bias will depend on the length of time that animals are active each day. During summer, when moose are active more then 12 hours per day (Cederlund 1989, Bevins et al. 1990, Van Ballenberghe and Miquelle 1990), this bias would be exacerbated. For example, suppose that location attempts are made at 10-minute intervals when a moose is active for 12 hours each day and activity reduces success of location attempts from 88% to 69%. In each day, 68 of 77 location attempts would be successful while animals were inactive, and 53 of 77 location attempts would be successful while animals were active, an 8% bias against locations where moose were active. During winter, when moose are active about 8 hours per day (Risenhoover 1986, Cederlund et al. 1989, Miquelle et al. 1992), the bias would still affect interpretation of habitat use; 84 of 96 location attempts would be successful while animals were inactive, and 33 of 48 location attempts would be successful while animals were active, a 7% bias against locations where moose were active.

We believe that our classification of moose as inactive during each 10-minute interval is conservative. From direct observation of a moose wearing a GPS collar, we know that low activity counts are more frequent during an active period than high activity counts are during inactive periods (Moen et al. 1996a). Because we were more likely to classify inactive periods as active than active periods as inactive, it is possible that we underestimated the reduction in frequency of obtaining successful location attempts when moose are active. When collars were carried on a backpack at a speed of 3-4 km / hour through forest canopy only 50% of location attempts were successful (Edenius 1997), compared to our estimate of 69% of location attempts being successful on free-ranging moose in unknown cover types.

A second factor that may affect the probability of obtaining successful locations when moose are active is vegetation type. Movement did not affect the probability of obtaining a successful location on a moose that foraged under thin or open canopy conditions (Moen et al. 1996b). In contrast, the northern Minnesota study area is a national park with no tree harvesting, and there have been no recent fires. Therefore, these moose were foraging in areas with mature trees and thicker boles that may interrupt GPS signal acquisition. GPS collars may underestimate use of mature stands relative to more open habitat types (Dussault et al. 1999), making it possible that the vegetation effect acts to counteract the activity effect on location success, at least for moose. How to address this problem is one of the difficult questions that remains to be answered when interpreting habitat use from GPS collar data.

Increased success of GPS location attempts in collars placed on white-tailed deer that were active (Bowman et al. 2000) suggests that the performance of GPS collars should be tested for each target species in different vegetation types. It is possible that the increased success of location attempts in active white-tailed deer is due to a relatively open canopy in that study area, as noted by Bowman et al. (2000). This would be consistent with the original report that activity did not affect the probability of obtaining a GPS location (Moen et al. 1996b) which was further refined in this manuscript based on additional data.

The precision of GPS locations depends on numerous factors that must be identified in order to make valid comparisons among GPS studies (Moen et al. 1998). Precision of GPS locations is dependent on topography, vegetation, animal behavior, the GPS system status, and decisions made by the investigator. Satellite acquisition by the collar and by the base station are the primary determinants of precision of GPS locations (Moen et al. 1997). Under ideal conditions, 95% of positions can be within 12 m of the true position (Moen et al. 1997). In areas of high relief or under a dense tree canopy, signals from the GPS satellites can be blocked, leading to acquisition of fewer satellites by the GPS unit and a consequent loss of precision in GPS locations. Activity of the animal wearing the GPS collar may also reduce acquisition of satellites (Table 1) leading to a further loss of precision.

A final decision on precision is made with the HDOP cutoff for switching from a 3-dimensional to a 2-dimensional position, and ultimately to a failed location attempt. For example, the investigator needs to decide if a 10% increase in successful 3-dimensional locations is more important than the 12 m increase in the 95% CEP of these positions. In practice, because 3 or 4 satellites are obtained in most location attempts when collars are on free-ranging moose, a conservative estimate of 50% of positions being within 10 m and 95% of locations being within 25 m may be used for differentially corrected locations obtained from GPS collars deployed on free-ranging moose when HDOP is ≤ 20. Pending further study, these may also be reasonable estimates of the precision of GPS locations that are not differentially corrected when SA is not in effect. Later generations of GPS collars may improve in both accuracy and in ability to obtain successful locations as technology advances.

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